# EFFECTS OF THE SUMMER OF 1989 ON THE PHENOLOGY OF THE WART-BITER, *DECTICUS VERRUCIVORUS* (L.), (ORTHOPTERA: TETTIGONIIDAE) IN BRITAIN

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## SUMMARY

The summer of 1989 was unusually dry, warm and sunny. In comparison to the two previous years, adult recruitment in a population of the rare bush-cricket, *Decticus verrucivorus* (L.), was completed four to five weeks earlier, and there was less variance between individuals in the timing of final ecdysis. Nymphal densities were lower in 1989 than in 1988, while the converse was true for adult densities suggesting that nymphal survival may have been enhanced by the warmer weather of 1989. There were no consistent differences between years in four measures of adult size.

## INTRODUCTION

The spring and summer of 1989 were unusually dry and sunny, with higher than average temperatures throughout much of the British Isles, but particularly in southern England (Northcott, 1990a, 1990b). The period May to October 1989 was equal fourth warmest, since records for central England began in 1659. There were more sunshine hours in this period than in any year since 1909 (Jones & Hulme, 1990). The atypical weather may have been expected to influence the developmental biology and survival of many species of invertebrates. However, with a few exceptions, quantitative evidence for most orders are sparse, mainly because base-line year-to-year observations are lacking.

The Butterfly Monitoring Scheme, along with the Rothamsted suction and light traps provided comparative data for the macro-lepidoptera, aphids and moths (Ward & Cannell, 1989; Ward, 1990). Although many species emerged early and attained high population densities, others were adversely affected by the lack of moisture. Overall, the responses of individual species were difficult to predict. However, a group of invertebrates likely to have benefitted from the weather of 1989 are those thermophilous species which are at the northerly edge of their range in southern Britain. The 'wart-biter' bush-cricket, *Decticus verrucivorus*, is one such species (Marshall & Haes, 1988; Cherrill & Brown, 1990a).

This paper quantifies the effects of the weather of 1989 on various aspects of the wart-biter's post-embryonic biology, using data from 1987 and 1988 (Cherrill & Brown, 1990a, and also unpublished data) as a basis for comparison. The results provide an insight into the extent to which the phenology of a large and rare thermophilous species at the edge of its range is constrained by the weather in more 'typical' years.

## SPECIES, STUDY SITE AND WEATHER

In Britain, four wart-biter populations are known in southern England. Eggs hatch in mid-April, after passing a minimum of two winters in diapause (Ingrisch, 1984). There are seven nymphal instars and adults can survive until early October (Cherrill & Brown, 1990a). The study population occurs on contiguous south- and east-facing

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Table 1. Meteorological data for the period April–October (1974–1989) from near Brighton, East Sussex.

| | | April | May | June | July | August | Sept. | Oct. |
|---|---|---|---|---|---|---|---|---|
| Total | 1987 | 169.1 | 217.6 | 155.5 | 206.6 | 190.4 | 146.8 | 99.6 |
| sunshine | 1988 | 153.9 | 179.6 | 114.0 | 184.3 | 203.8 | 155.4 | 121.8 |
| (h) | 1989 | 164.6 | 329.0 | 288.0 | 289.9 | 271.7 | 147.7 | 116.7 |
| | 1974–1986 | 173.5 | 197.7 | 212.7 | 217.2 | 211.3 | 151.1 | 111.2 |
| Total | 1987 | 61.0 | 39.3 | 114.9 | 143.1 | 65.3 | 46.6 | 239.1 |
| rainfall | 1988 | 46.5 | 38.1 | 7.2 | 75.3 | 40.8 | 47.3 | 88.2 |
| (mm) | 1989 | 61.1 | 2.9 | 26.9 | 47.5 | 26.6 | 57.6 | 86.5 |
| | 1974–1986 | 45.5 | 56.8 | 54.5 | 44.9 | 62.4 | 82.0 | 98.7 |
| Mean daily | 1987 | 10.1 | 10.7 | 13.2 | 16.2 | 16.0 | 14.5 | 11.5 |
| temp. | 1988 | 8.2 | 12.4 | 14.1 | 14.4 | 15.7 | 14.1 | 12.0 |
| mode (°C) | 1989 | 6.9 | 14.1 | 15.7 | 18.4 | 17.0 | 15.6 | 12.7 |
| | 1974–1986 | 7.8 | 11.0 | 14.3 | 16.3 | 16.2 | 14.0 | 11.0 |

unimproved chalk grassland in East Sussex (see Cherrill & Brown, 1990b, 1991). During the study, the height profile of the vegetation remained stable under a regime of light autumn/winter grazing. Weather data for April–October were obtained from a site 5 km distant and are summarized in Table 1. Similar meteorological conditions prevailed over much of southern England (Northcott, 1990a, 1990b).

## Methods

The population was monitored on five 15-m-wide transects. Three on the east-facing slope were 55–60 m long, while those facing south were 110 and 115 m long. The post-embryonic stages were monitored from late June in 1987 and from mid-April in 1988 and 1989. In each year, monitoring continued until early October. Different methods were used for monitoring early instar nymphs (1988 and 1989 only) and late instars/adults (1987–1989). From mid-April to late May and early June in 1988 and 1989, densities were estimated on the three east-facing transects only. A 1-$m^2$ box-quadrat was repeatedly placed on each transect at co-ordinates selected at random. In 1989, 30–40 quadrats were taken on each transect at intervals of 3–11 days, depending on the weather. A similar regime was followed in 1988 (see Cherrill & Brown, 1990a). From 1 June (1987–1989), a walk survey method was used to estimate densities of late instars and adults on each of the five transects. Surveys were performed at intervals of approximately two weeks. The technique involved slowly walking across the central 5-m-wide core of each transect, at right angles to its length and at intervals of 0.75 m (see Cherrill & Brown, 1990a, for details). The numbers of wart-biters of each developmental stage in box-quadrats, and on each transect were recorded. All observations were made in warm sunny conditions and wart-biters were released at their points of capture.

In addition to the dates on which quantitative estimates of population density were made, the study site was visited two or three times weekly in 1987 and 1988 (but less frequently in 1989). On these occasions, the developmental stages of any wart-biters seen were noted. These data provided further information for assessing the timing of adult recruitment.

In 1987, the length of hind femur, forewing and ovipositor of adults of each sex were recorded. In 1988 and 1989, the length of pronotum was also measured. All measurements were made to within 0.5 mm in 1987 and to within 0.01 mm in 1988 and 1989 (methodology in Cherrill & Brown, 1990a). Student's *t*-test (modified for

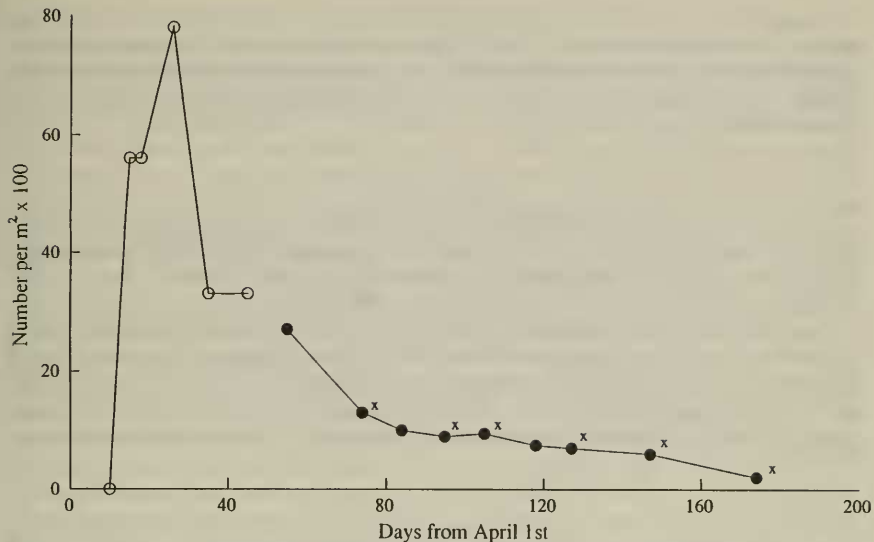


Fig. 1. Temporal variation in mean densities of *D. verrucivorus* on a south-facing slope (x) (walk survey estimates) and an east-facing slope (○, box-quadrat estimates; ●, walk survey estimates) in 1989.

unequal variances as appropriate) was used to compare means between years (Bailey, 1959).

## Results

Here, data from 1989 are presented in detail, while those from 1987 and 1988 are summarized from Cherrill & Brown (1990a).

### *Temporal variation in density and timing of egg hatch*

Figure 1 shows the estimated density of the post-embryonic stages throughout their period of occurrence in 1989. Most box-quadrats (i.e. 96%) contained no wart-biters and none yielded more than one nymph. Standard deviations for these means are consequently omitted from Figure 1. Observations from transects with the same aspect have been pooled to give overall estimates of mean density for east- and south-facing transects. The pattern of variation in densities between transects of the same aspect paralleled that seen in 1987 and 1988 (see Cherrill & Brown, 1990a).

The first nymph was recorded on 15 April and the greatest density was found on 26 April (Figure 1), at which time only first instar nymphs were present. The peak nymphal density in 1988 was recorded on 25 April, indicating that egg hatch occurred on approximately the same date in each year. However, in 1989 the peak mean density was 45% lower than that in 1988. No comparable data on nymphal density are available for 1987.

As in 1987 and 1988, adult densities in 1989 were relatively stable, but in both 1988 and 1989 densities fell dramatically during nymphal development. Adult densities in 1989 were very similar to those recorded in 1987, and in both years there were no obvious differences in densities between east- and south-facing slopes.

In comparison, adult densities on the east- and south-facing slopes respectively were around 75% and 30% lower in 1988. These data contrast with the greater nymphal densities in 1988, and tentatively suggest that, at least on the generally cooler east-facing slope, nymphal survival may have been greater in the warmer weather of 1989 than in 1988.

### *Development*

In 1989, recruitment from the final instar to adult was complete four to five weeks earlier than in either 1987 or 1988 (Table 2). Development in 1989 was also more synchronous. Nymphs and adults co-occurred for at least 18 and 34 days in 1987 and 1988 respectively, but fewer than 14 days in 1989.

The more synchronous and rapid development in 1989 can be attributed to the consistently warmer and sunnier weather. The differences between the timing of adult recruitment in 1987 and 1988 were more subtle (Table 2). The first adult appeared slightly earlier in 1988 than in 1987. However, the weather in July 1988 was unusually cool and cloudy, prolonging the temporal overlap of nymphs and adults in that year (Tables 1 and 2).

### *Body size*

Measurements of adult body size taken in 1987 (unpublished), 1988 (from Cherrill & Brown, 1990a) and 1989 are summarized in Table 3. Overall there were no consistent between-year differences in the four measures of adult size. Females had significantly longer ovipositors in 1989 than in 1987 or 1988; while male forewings were shorter in 1987 than in either other year. Neither sex differed between years for any other dimension measured ($P>0.05$ in all pair-wise comparisons).

Table 2. Dates on which the first adult and last nymph of *D. verrucivorus* were seen in three years.

| Observation | 1987 | 1988 | 1989 |
|---|---|---|---|
| First adult | 8.vii | 1.vii | 28.vi |
| Last nymph | 25.vii | 3.viii | 14.vi |

Table 3. Linear measures of body size for adult *D. verrucivorus* in three years. Figures are means with s.d. in parentheses. All measurements in mm. Figures with the same letter are significantly different ($P<0.05$).

| Year | Sex | Hind femur | Pronotum | Forewing | Ovipositor | N |
|---|---|---|---|---|---|---|
| 1987 | M | 26.81 (1.19) | — | 20.71[ab] (1.38) | — | 42 |
| | F | 28.73 (1.42) | — | 20.61 (1.40) | 19.05[c] (1.07) | 31 |
| 1988 | M | 26.50 (1.00) | 7.64 (0.41) | 21.54[a] (1.50) | — | 26 |
| | F | 28.43 (0.87) | 8.21 (0.31) | 20.28 (1.71) | 18.82[d] (0.71) | 27 |
| 1989 | M | 26.73 (0.77) | 7.65 (0.26) | 22.05[b] (1.39) | — | 8 |
| | F | 28.36 (1.12) | 8.11 (0.35) | 21.03 (1.39) | 19.91[cd] (1.09) | 15 |

## Discussion

*Decticus verrucivorus* is at the edge of its range in southern England. Previous observations at the present study site, near Brighton, Sussex, have suggested that its northerly limit is determined primarily by its thermophilous nature and climate (Cherrill & Brown, 1990a, 1990b). However, the extent to which different aspects of the wart-biter's life-history are constrained by environmental factors (notably the weather) in 'typical' years is poorly known. Previously, Cherrill & Brown (1990a) reported no difference in adult hind femur length, and only a slight difference in the timing of adult recruitment, between 1987 and 1988 (Tables 2 and 3). This may have reflected the relatively slight difference in the weather in these two years (Table 1). Here, however, new data from the unusually warm spring and summer of 1989 are presented for comparison, along with additional unpublished data on body size in 1987.

Ingrisch (1978) demonstrated that nymphal development rates are temperature-dependent in the laboratory, being most rapid at 33°C and ceasing below 20°C. None the less, the magnitude of the effect of the weather on developmental rates in 1989 was striking. Adult recruitment was completed four to five weeks earlier than in either 1987 or 1988 (Table 2). In contrast, there was little evidence that adult body size was affected by the difference in weather between years (Table 3).

In most years, the potential longevity of the adults must be severely constrained by meteorological conditions. Moreover, adult survival is high (Figure 1; Cherrill & Brown, 1990a) suggesting that the timing of adult eclosion may be an important determinant of reproductive success. Haes *et al.* (1990) argued that variation in reproductive success is the principle cause of fluctuations in population size in *D. verrucivorus* at the study site. Between 1967 and 1987, the numbers of adults in a given year were found to be strongly correlated with the number of sunshine hours in the summer two years before, but not with the weather one year before or in the year of observation (Haes *et al.* 1990). This was interpreted as the result of a two-year embryonic phase, and the dependence of reproductive output on sunshine and high temperatures. Implicit in this interpretation is that the survival rates of the egg and nymphal stages are relatively stable from year to year (at least in comparison to fluctuations in reproductive output).

To date, information on fecundity and egg survival are lacking. Data on nymphal densities are available for 1988 (Cherrill & Brown, 1990a) and 1989 (Figure 1), yet caution must be applied in equating changes in density with survivorship. Given this constraint, the smaller reduction in nymphal densities in 1989 than 1988 tentatively suggests that nymphal survival may have been enhanced by the warmer weather in that year. Such an observation would be typical of other ground-dwelling Orthoptera (Dempster, 1963; Pickford, 1966; Atkinson & Begon, 1988) and hence could be expected in the present study.

Due to the wart-biter's minimum two-year embryonic phase (Ingrisch, 1984), the full impact of the weather of 1989 will not be evident until 1991 onwards. The work of Haes *et al.* (1990), along with the direct evidence of early adult recruitment in 1989, suggest that a large number of eggs will hatch in 1991, thereby giving the potential for a large adult population. However, recent changes in the spatial heterogeneity of the vegetation may prevent realization of this potential. The drought conditions of 1989 greatly reduced grass growth. This factor, in combination with overgrazing by livestock in late 1989 and early 1990, resulted in a uniformly short turf throughout 1990 (Brown, Shaughnessy & Cherrill, unpublished). As a consequence, very few late instar nymphs and adults (which require dense tussocks) were recorded in 1990 (Cherrill & Brown, 1990b, in press, and also unpublished data). At the time of writing, in early 1991, the vegetation is still short, and it remains uncertain whether the potential for a large population of adults will be realized in the absence of significant rainfall (allowing rapid grass growth).

Data from the continued monitoring of the population in 1990 and 1991 will be analysed in detail elsewhere. However, these initial observations emphasize the need for a flexible grazing regime, if the potential demographic benefits of hot, dry years are to be realized.

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